

On the Philosophy and Methods used to reconstruct Tertiary Vegetation

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Historical interpretations may be offered from plant geography, phylogeny and other studies on living plants as well as the fossil record. Lange (1982) considers that in theory, palaeovegetation reconstructions should result in a single interpretation satisfactory to all, but in practice this is not the case.

This paper examines the lines of evidence used to reconstruct Tertiary vegetation, what each method can do, and just as important, what each method cannot do. It does not present a reconstruction of the Tertiary vegetation; that may be found in Martin (1982). The application of the principle of uniformitarianism with respect to analogy and to basic physical and biological processes is also discussed. This evidence is crucial to the interpretation of fossil evidence.

The fossil record, when used to reconstruct Tertiary vegetation, can do three things which no other line of evidence can do, viz., (1) provide a time control, for fossils can be dated by any of a number of methods, (2) reveal extinct taxa and lineages, and (3) show that taxa have occupied regions where they no longer grow. All three are essential in the reconstruction of Tertiary vegetation.

Plant geography, phylogeny, growth rhythms and other lines of evidence from living plants may be used to suggest hypotheses which require testing by independent evidence. If the hypothesis is an historical one, then the fossil record is an important source of independent evidence. The reconstruction of the Tertiary vegetation from fossil evidence is a speculative process, but to use these other lines of evidence from living plants for such reconstructions is to speculate upon mostly untested hypotheses, and this is not acceptable.

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INTRODUCTION

There is an intrinsic interest in how the present state of the flora and vegetation came to be. It is well recognized that historical factors play an important part, but how does one deduce the history of a flora and vegetation? On one hand, studies from a wide range of botanical disciplines have, at some time, offered historical hypotheses as an explanation of the observations being reported. This practice is most frequent in biogeography and plant ecology, but it also occurs in phylogeny, taxonomy, cytology and plant physiology (e.g. growth rhythms). The historical hypotheses postulate changes through time although the evidence is gleaned from a single instant of time, the present. On the other hand, palaeobotanists present historical hypotheses from fossils which are records of life during past ages. Lange (1982) considers that theoretically, the reconstruction of the Tertiary vegetation should result in a single interpretation which is satisfactory to all, but in practice, this is not so. The hypotheses generated from the different disciplines are frequently at some variance with each other.

This paper examines the philosophy behind the methods used to reconstruct Tertiary vegetation. It examines the strengths and weaknesses of the different lines of evidence. Selected examples are used to illustrate the principles discussed. It is not intended to present a reconstruction of the Tertiary vegetation in this paper, but this may be found in Martin (1982).

Throughout this paper, speculation is used in the sense that it is based on evidence; inference is used in a sense that it is not so constrained. Inference may draw

upon several lines of argument which appear reasonable but for which direct connection has not been demonstrated.

UNIFORMITARIANISM

All aspects of palaeobotany and palaeoecology, and indeed all historical sciences, rely on the principle of uniformitarianism, i.e., the present is the key to the past. However, there is evident confusion as to how this principle should be applied. On the one hand, basic physical and biological processes are assumed to have remained the same through time and an understanding of the past is sought in terms of these modern processes (Rymer, 1978). On the other hand, analogy is used to match past patterns of distribution with those of today. In attempting to use analogy, Quaternary palaeoecologists have found that some plant communities of 10,000 years ago have no modern counterparts (Davis, 1978). Tertiary plant communities, the youngest of which are two million years old, are unlikely to exist today without significant modification. Some Tertiary environments may have been quite unlike any experienced today and are likely to have produced plant communities with features not known today. Clearly, analogy has severe limitations in reconstructing the Tertiary vegetation.

The question of Tertiary forests in the high latitudes, before the poles became glaciated, provides an illustration of the two ways the principle of uniformitarianism may be applied. The inhospitable polar regions are quite unsuitable for tree growth today, so there are no modern analogues. The Early Tertiary fossil record, however, is unequivocal. Silicified wood and stumps show that trees once grew in both arctic and antarctic regions. On Ellesmere Island (present and palaeo-latitude about 77-82°N, i.e. latitudes in these regions of the northern hemisphere have not changed), the Early Tertiary angiosperm trees were deciduous and petrified wood shows sharply-defined rings caused by seasonal growth. An unusual leaf gigantism is inferred from modern studies to result from almost continuous photoperiod. There is also relatively low diversity in these assemblages (Hickey, 1981). Reptilian assemblages indicate an equable climate with winters that rarely suffered freezing temperatures (Estes and Hutchinson, 1980). Angiosperms predominate in Early Tertiary floras of Spitsbergen (present and palaeo-latitude about 76-80°N) and they are almost entirely broadleaved, deciduous species. A bivalve and the foraminifera indicate a cool temperate climate with occasional wintery snowfall and light frosts. The coniferous flora divides into two groups: (1) those genera which are frost tolerant but cannot reproduce under a cool temperate climate, and (2) genera which are extremely sensitive to cold so that the younger branchlets are killed by light frosts (Schweitzer, 1980).

The basic biological problem involved here is survival during the long polar winter. The evidence indicates that temperatures were not severely limiting in the Early Tertiary but months of almost continuous darkness would be a serious constraint. However, dormancy would allow the plants to avoid these adverse conditions. Mammalian and reptilian faunas are found also in the Early Tertiary Ellesmere Island deposits. Animals become dormant during adverse conditions as well. Winter dormancy is considered energetically more practical for reptiles (even for those whose modern relatives do not practise it) than is the ability to function under optimal temperatures lower than that found in those groups today (Estes and Hutchinson, 1980).

Evidence of Tertiary vegetation in the high southern latitudes is limited (for a review of antarctic vegetation, see Truswell, 1982), but there is a remarkable Early Cretaceous fossil forest, where stumps and trees have been preserved *in situ* by volcanic muds, at palaeo-latitude 69-75°S (Jefferson, 1983). These are all gymnospermous trees

for angiosperms were just evolving about this time, but the basic biological processes for tree growth are the same as for angiosperms, and, indeed, the silicified wood has been examined according to the standard methods of tree-ring analysis.

Undoubtedly, there is much to be learned about life in the polar regions when they were unglaciated and this topic is not without controversy. However, analogy can do little to further our knowledge which will rely on the application of basic biological processes. It is just as important to apply basic biological processes to less extreme examples, such as the Tertiary in lower latitudes, for even if an apparent analogue is found, the comparisons are, at best, superficial. Experimentation into these basic processes under simulated environmental conditions could prove fruitful.

The physical environment of a relatively warm polar climate has no analogue today. On the one hand, some extraordinary mechanisms have been invoked to account for this extraordinary climate. A change in the inclination of the earth's axis of rotation is one such mechanism. Wolfe (1978) advocates such a mechanism but admits that the changes required to produce the temperatures indicated by the Eocene fossils in polar regions would have had very serious consequences on the earth's crust. In addition, with no inclination, there would be no seasonality, and at the poles, the sun would have been about a dozen or so degrees above and below the horizon on each day and night which, coupled with a forested landscape, would have resulted in very low light intensities on the forest floor (McKenna, 1980). It has also been suggested that the solar radiation received by the earth has been greater in the past, although the solar 'constant' has only varied within about 1% of its present value during the last century. However, in order to produce the Eocene temperatures indicated by fossils in polar regions, the increase in solar radiation would be such that the tropics would be baked to death (McKenna, 1980). Clearly, extraordinary propositions of this kind create more problems than they solve.

On the other hand, the warmer polar climates may be explained in terms of physical processes which operate today, for example, heat transfer from the equator to the poles via oceanic currents. The models of Frakes and Kemp (1973) indicate that the warm equatorial currents could penetrate to higher latitudes along the eastern coasts of the continents during the Early Tertiary, before the southern circumpolar current became established. Their estimates of high latitude Eocene temperatures do not conflict with those indicated by the fossil plants (Frakes and Kemp, 1973). Barron *et al.* (1980) model the effect of changes in continental position on the distribution of land and sea and its influence on the energy budget through altered albedo. Their models indicate that small variations in the radiation balance result in dramatic climatic changes. Climatic modelling is in its infancy, but it is based upon processes which may be observed and measured in operation today, and should prove fruitful to the understanding of environments totally outside of present experience.

In practice, both ways of applying the principle of uniformitarianism are necessary, although the limitations of analogy should be obvious. The attribution of ecological tolerances of modern representatives to the fossil taxon is probably an unavoidable analogy, although numerous examples of closely-related modern taxa with different ecological tolerances could be quoted. However, if the ecological tolerances of each taxon in the fossil assemblage are considered together with all the abiotic information of the sediments, and together with the basic physical and biological processes approach, a sound reconstruction of the fossil ecosystem can be achieved.

THE NATURE OF FOSSIL EVIDENCE

The use of basic physical and biological processes to reconstruct past floras and

vegetation results in a more general and less specific interpretation (Rymer, 1978) which cannot match the precision of results from the study of living plants. This may be seen at almost every level. For example, fossil populations may be circumscribed and form-species described, but they are rarely equivalent to natural species. With pollen, the fossil form-species may be equivalent to a genus but more frequently, it encompasses several related genera, although not necessarily all the species in these genera. Pollen may be identifiable only to family or a higher level of the taxonomic hierarchy. In other words, the fossil unit, the form-species is not equivalent to any unit in a natural classification of living plants. The type of vegetation may be deduced from the fossil pollen assemblage, but only to a fairly general level, e.g. the formation or vegetation-landform unit (Birks and Birks, 1980).

Fossil assemblages may be dated with varying degrees of certainty/uncertainty. For Tertiary plants in Australia, the most common method of dating involves identification of the pollen assemblage with a described palynological zone which has been dated using independent evidence. An absolute chronology, i.e. radiometric dating (usually potassium-argon) is rarely possible for it requires basalts and fossiliferous sediments to be interbedded. Such requisites are rarely fulfilled in Australia.

The fossil record is often dismissed because it is incomplete. Admittedly, it is incomplete and will remain so, even after many more new discoveries and studies. Paul (1982) shows that the fossil record is much less incomplete than generally accepted. Its incompleteness is largely irrelevant if reconstructions are confined to the known organisms. In any case, every branch of science is incomplete as new evidence will come to hand and old evidence will be viewed with new insight. The fossil record is no different from any other branch of science in this respect. Its incompleteness should not be used as an excuse to dismiss the fossil evidence.

LINES OF EVIDENCE

Palaeobotany/palynology

Fossil spores and pollen are abundant, widely dispersed, and can be recovered in sufficient quantities for routine quantitative evaluation. Many sediments, including those obtained from boreholes, are suitable for palynology; relatively few can be used for analysis of macrofossils for which outcrops are usually required. Once recovered, the fossils (leaves, pollen, wood etc.) must be identified, and there are many pitfalls associated with this procedure. Such identifications produce a fossil assemblage that is an indicator of the floristics for the region. The major problem is in the interpretation of such fossil assemblages into the type of vegetation that might have existed. The interpretation of pollen assemblages relies primarily on species composition and comparisons with living relatives, whereas leaf assemblages may indicate the type of vegetation through a foliar physiognomic classification (e.g. that of Webb, 1959), quite independent of floristics.

There is a wealth of experimental and observational data on modern pollen production, liberation, dispersal, deposition, sedimentation, preservation, deterioration and redeposition which is used as a basis for the interpretation of Quaternary pollen diagrams (see West, 1971; Birks and Birks, 1980). While the examples in these references are almost entirely from the Quaternary of the northern hemisphere, many of the general principles are applicable to Australia and to the Tertiary. Specific examples applying to Australian taxa may be found in almost all of the papers on Australian Quaternary pollen analysis and there are some studies devoted entirely to modern pollen deposition (e.g. Kershaw and Hyland, 1975).

Papers on New Zealand Quaternary and modern pollen studies also contain much that is relevant to the Australian Tertiary (see Martin, 1984).

Quaternary palaeoecologists reconstruct plant communities using one or more of the following broad methods (Birks and Birks, 1980: 231):

(1) The statistical approach leading to the delineation of recurrent groups.

(2) The application backwards in time of known ecological and sociological preferences of taxa. Those with a well-defined narrow ecological tolerance can be used as indicator species.

(3) The comparison of fossil pollen spectra with modern pollen studies from known vegetation types.

The last two methods rely on finding modern analogues. The reconstruction of Tertiary vegetation utilizes mainly the second method, but in a more general way than that used in the Quaternary. The statistical approach, where a mathematical method is used to calculate some measure of interspecific association may be used quite independent of modern analogues, or if analogues are used then this method may show the fossil assemblages for which there are no analogues (see Birks, 1976). Luly *et al.* (1980) have used this method to delimit recurrent groups in the Australian Tertiary, and wisely, without any attempt to match them with modern analogues.

There appear to be no similar 'guide lines' for the interpretation of macrofossil assemblages. Relatively little experimental work has been done to elucidate the extent of, or the processes involved in, the transport, sorting, degradation and deposition of macrofossils. Spicer (1981) considers that much has been taken for granted in the interpretation of macrofossil assemblages and even the most basic assumptions must be tested.

Spicer (1981) chose a small lake with a stream forming a delta advancing over the lake bottom, for a detailed investigation of leaf deposition. Leaves accumulate on the bottom of the lake. The stream entering the lake transports leaves into it, but because of the difference in settling rates, most of the mineral particles settle first and the leaves settle out on top. In this way, two leaf beds of different provenance are being formed at the same time, viz. (1) the lake leaf bed, with leaves from species growing around the margin and leaves blown off the top of the canopy and (2) the delta leaf bed, with leaves from species growing on the delta and those transported in by the stream. These two leaf beds may contain different species assemblages. This is only one example of leaf accumulation, but it illustrates the importance of knowing the conditions under which macro-fossils accumulate.

Biological degradation is an important factor in the preservation of leaves. Invertebrates attack leaves already affected by microbial activity. Decomposition by fungi is more devastating than bacterial activity. There is evidence of differential attack, organisms of decay preferring leaves with a high nitrogen and phosphorus content. The content of lignin and antifungal compounds, e.g. condensed tannins, in leaves is also important in determining the rate of decay. Rapid burial by inorganic sediments ensures better preservation (Spicer, 1981).

Quaternary palaeoecologists may investigate macrofossils using much the same methods as those for pollen. These macrofossils are mainly fruits and seeds, and a 'seed diagram' may be constructed in much the same way as a pollen diagram. Surface samples of lake sediments are used to investigate modern representation and dispersal of the macrofossils. Where both pollen and macrofossils have been studied from the same sediments, each complements the other and a much better reconstruction of the vegetation is obtained.

Some macrofossil assemblages accumulate *in situ* and these afford excellent opportunities for reconstruction of the plant communities. Blackburn (1981) has

reconstructed some Miocene swamp vegetation from macrofossils in the Latrobe Valley brown coals. Reconstructions from palynology (Luly *et al.*, 1980) contain much that is complementary and there is a core of evidence in general agreement. Hill (1982) has compared the Eocene macro- and micro-floras of Nerriga. Some of the evidence may be complementary, but the lack of taxonomic determinations make comparisons difficult. Of the 25 leaf taxa circumscribed, only 5 have been identified with living representatives and only one of the five is an angiosperm. Not all of the pollen is identifiable either. Part of the difficulty of identifying older Tertiary fossils involves the lack of relevant reference sets. However, Hill used leaves from several thousands of Australasian species of angiosperms for the one identification, so larger reference sets are unlikely to overcome this difficulty. It could be that many of the early Tertiary angiosperms are extinct, or that evolution has so altered the character of leaves that they cannot be identified with extant taxa. There is no reason to assume that evolution has proceeded at the same rate in pollen and leaves (Hill, 1982), particularly since pollen is believed to be 'conservative' in this respect.

With leaves, however, a foliar physiognomic classification is possible, e.g. that of Christophel and Blackburn (1978). The reference classification of Webb (1959) is based upon sun leaves, the smallest of the mature leaves. Fossil assemblages are likely to contain a mixture of sun and shade leaves, hence the degree of tropicality is likely to be somewhat inflated (Webb, *pers. comm.*).

The best reconstructions of the Tertiary vegetation will result from the investigation of both macro- and micro-fossils. Not all deposits are suitable for comprehensive investigations of this kind, indeed few are capable of producing the excellent evidence obtained from the Latrobe Valley brown coals. Nevertheless, evidence from less comprehensive investigations is of value, but it is important to remember its limitations and bias.

Plant geography

Classical plant geography seeks to explain the cause of present distributions from evidence inherent in these distributions. This practice is of very long standing and has relied on the area of origin and dispersal concept originally proposed by Darwin. In this model, a taxon spreads out from its area of origin by dispersal, expanding its distribution with time. This expansion may be stopped or channelled by barriers to dispersal. Recently this concept has been challenged by the vicariance model in which a widespread distribution becomes fragmented. The cause of this disjunction is frequently attributed to continental drift. (For a full account of these topics see Nelson and Rosen, 1981). Both models, however, rely primarily on the present distribution of the groups concerned. It is freely admitted (e.g. Stott, 1981) that many 'external' factors influence distributions, e.g. changes in climate, geology and other biotic factors, which would disrupt or obliterate the distributions expected on these theoretical models. There are, however, many phytogeographic studies which pay scant attention to such 'external factors'. Many of the studies also pay little attention to the environment and ecology, and historical explanations are offered for distributions which may be controlled by these factors.

Just how much the original premises and methods influence conclusions may be seen in two papers presented in the symposium 'Bridge and Barrier: The natural and cultural history of Torres Strait' (Walker, 1972). In the first, Hoogland (1972) interprets plant distributions by the classical historical biogeographic method, i.e. a monophyletic origin of a taxon and its subsequent increase in area which, theoretically would constitute concentric circles, but which are modified by topography and other features of the habitat. After an analysis of family, generic and species distributions for New Guinea and Australia, the latter sometimes divided along the Tropic of

Capricorn, Hoogland concludes that Torres Strait is a distinct barrier to dispersal and anomalous distributions which transgress the Strait are explained when habitat factors are taken into account. It is hardly surprising that these comparisons produce marked differences, since approximately half the area of Australia north of the Tropic of Capricorn falls within the arid zone, whereas New Guinea is mostly rainforest and has no arid zone.

In the second example, Webb and Tracey (1972) adopt an ecological approach. Structurally and physiognomically similar communities are believed to reflect equivalent physical environments, so pairs of communities occupying analogous habitats, one from northern Australia and one from New Guinea are compared. Within Australia the structural and floristic differences between adjacent rainforest and sclerophyll forest are far greater than related community pairs widely separated by Torres Strait. The infertile soils of Cape York Peninsula do not permit the growth of rainforest except in the most favoured and small habitats. Where rainforest does grow on Cape York Peninsula, it is closely related to that in New Guinea. Thus the major barrier is the change in soil type which, for the most part, coincides with Torres Strait. The water gap of the Strait is hardly any barrier to dispersal if there is a suitable environment for growth.

These two studies illustrate how an historical explanation may be offered for distributions which are really the result of ecological causes. The failure of many biogeographical studies to take account of ecology and the habitat is a serious shortcoming.

Traditionally, the tropical elements in northern Australia (i.e. many rainforest species), have been regarded as recent immigrants from the Indo-Malaysian area (the 'invasion theory' outlined by Barlow, 1981). On distribution alone, this appears a reasonable proposition, as many of the groups are much better represented in the island chain to the north. It is only recently that the long history and wide distribution of rainforest in Australia all through the Tertiary, as shown by the fossil record (Martin, 1978, 1981) has been accepted. Herbert consistently opposed the immigration view (Barlow, 1981) partly for ecological reasons and partly because of the fossil record. Writing fifty years ago, Herbert (1933) gave his reasons thus: the Australian palaeotropical (= tropical) element is easily recognizable as distinct from the typical Australian element. Its distribution is restricted primarily by climatic factors although it has a wide range in Australia. Formerly it covered a much greater area, as the fossil record from New South Wales and Victoria indicates, and its present area represents a considerable contraction of its territory (Herbert, 1933). It is interesting to note that the fossil record, inadequate as our knowledge of it was fifty years ago, still showed essentially the same general pattern as it does today, to those who were willing to consider it.

The practice of seeking to explain the cause of distribution from evidence inherent in present distributions (called the retrospective method by Stott, 1981) developed long before there was a fossil record worthy of the name. Even if a fossil record is available, its general nature frequently cannot provide answers to specific questions about the pattern of distribution of individual taxa. While a number of Australian phytogeographic studies have made use of the fossil record, the inclination to relegate the fossil record to a supportive role, or dismiss it if it proves inconvenient, still exists. Barlow (1981) admits that *Acacia* is known in the fossil record only since the beginning of the Miocene, but 'it undoubtedly has had a longer Tertiary history in Australia'. No evidence for its undoubted history before the Miocene, nor reasons why it should have been absent from the fossil record before this time are given. One suspects that the fossil evidence does not agree with the author's notions, and is therefore simply written off.

The distribution of any plant species or group is determined ultimately by its ability to survive under the existing environment. But in addition to these limitations, distributions are also the product of historical factors, including past climates, geographics and floristics. Studies based on very simple models, such as the area of origin/dispersal or the vicariance model are unrealistic if they ignore the complex multifactorial nature of plant distributions. However, plant distributions may be used to suggest hypotheses which require testing with independent evidence. Indeed, many of the interpretations of biogeography should be viewed in this light: they are hypotheses which require testing. Unfortunately, the untested nature of the hypotheses is too frequently forgotten. On the one hand, it may take a long time to produce the required independent evidence. For example, although many biogeographical tenets effectively supported the hypothesis of continental drift, a fulfilling testing of this hypothesis required geophysical evidence and a programme of deep-sea drilling, some 50 years later. On the other hand, the evidence may exist, but be ignored for 50 years or more; for example, the invasion theory of the tropical element, discussed above.

Phylogeny

From cytological studies, Smith-White (1959) found that certain patterns of change in chromosome number run parallel in different families. In general, herbaceous taxa show more variation in chromosome number than woody taxa. For these woody taxa, differences in haploid numbers are said to be characteristic of genera rather than species. Smith-White concluded that the genera date from the early Tertiary. This date, however, is based on the fossil record of the Proteaceae, but one of the families he studied cytologically. There is a marked difference at the specific level in the hardwood floras of western and southeastern Australia which is inferred to be the result of long-standing isolation. Crocker and Wood (1947) postulate minimum isolation during the warm, moist Miocene period, so Smith-White infers that isolation has been effective since that time; hence he concludes that the species are post-Miocene and the genera pre-Miocene in origin. (For a more detailed summary of Smith-White's hypotheses, see James, 1981). Essentially, Smith-White viewed these patterns of variation in chromosome number, or cytological evolution, as some relative measure of time, and by an integration of the geological history as he knew it, arrived at an evolutionary interpretation spanning the Cretaceous and Tertiary.

Lange (1982) accepts the hypothesis that a relative age is displayed by the pattern of variation of chromosome number and uses phylogeny as one of his lines of evidence to reconstruct the Tertiary vegetation. James (1981), however, considers evidence accumulated since Smith-White formulated his hypothesis and shows that some of his assumptions do not hold. Smith-White's principle of the constant number of chromosomes within genera, and the diversity of chromosome numbers between genera amongst woody components of the Australian flora does not apply in the Casuarinaceae or Dilleniaceae; it is scarcely relevant in Myrtaceae, it is quite obscure in Epacridaceae and Rutaceae; it almost applies in Papilionaceae and it holds up quite well only in Proteaceae.

James (1981) presents an alternative hypothesis that cytoevolutionary change is more relevant to understanding genetic systems than in providing a basis for deducing past selection intensities. Chromosomal variation is frequently associated with changes in the breeding system towards inbreeding which conserves adaptive gene arrays but reduces heterozygosity. On the other hand, complete or relative chromosome stability is associated with effective cross pollination, and by inference, a high level of heterozygosity.

This hypothesis of James may provide a genetic explanation of some of the observed features of the fossil record. For example, proteaceous pollen first appeared

some 80 million years ago in the Late Cretaceous. In the Early Tertiary, there is a wealth of different forms, many of them undescribed. Many of these Early Tertiary forms became extinct by the end of the Eocene. There are some pollen forms, however, which occur in the Late Cretaceous, throughout the Tertiary and in living species (Martin, unpubl.). Some of the extinct forms may represent bursts of radiation in which adapted gene arrays are conserved, but because of their inbreeding tendencies, lack the genetic flexibility to survive change. Only the Proteaceae with relatively stable chromosome numbers, by virtue of their outbreeding and genetic flexibility, have survived to the present.

Other phylogenetic studies, such as that of the Proteaceae by Johnson and Briggs (1975), attempt to reconstruct the ancestral form of the family. The fossil record is far too inadequate for the reconstruction of a lineage, and they are thrown back on the comparative method using living forms. Their reconstruction of the phytogeographic history of the family makes as much use as is possible of the fossil record and the background of palaeogeography and palaeoclimatology, and should be regarded as an hypothesis about the place the family may have occupied in past ages.

At best, cytoevolutionary and other phylogenetic studies may suggest hypotheses which require testing by independent evidence. The fossil record is the most important source of independent evidence. Such hypotheses should not be used as though they are evidence for the reconstruction of the Tertiary vegetation. In any case, vegetation is not defined by the phylogenies of its component parts.

Growth rhythms

In a study of South Australian heath, Specht and Rayson (1957) found that the dominant species grew in the summer months, in contrast to the expected spring growth. This led to the conclusion that the growth rhythm of the heath 'is markedly out of phase with the annual climatic cycle' (Specht and Rayson, 1957). The geological history indicates that there was once a more humid, and probably warmer climate, so Specht (1973) concludes that the 'mediterranean-climate' flora of southern Australia is probably a relic of tropical origin. Thus modern rhythms are being used as evidence of the origin of the flora.

Specht and Brouwer (1975) list the growth periods of a number of species from different types of vegetation. In this context growth means the elongation of the stem tips and expansion of new leaves. It should be noted that not all the species in the one community grow at the same time. There is considerable variation and some species have two periods of growth, one in spring and one in autumn.

Growth is not confined to the expansion of the new leaves, although this phase is the most conspicuous and it may be the time of maximum growth. There is an annual cycle (Specht, 1975). Leaf decomposition is greatest in late winter and spring. If the major period of growth then follows, as it does with many sclerophyllous species, it may be advantageous to mineral recycling. It is thought that exotics with a spring period of growth may have a competitive advantage for minerals, except that they usually cannot become established in such infertile soils as support these sclerophylls (Specht, 1975). Thus Specht has provided an alternative hypothesis for the observed growth rhythms: they have some adaptive advantage to these infertile soils.

In South African sclerophyllous communities, there is wide variation of growing season although most growth occurs from late winter to early summer (Kruger, 1981). The diverse phenologies (i.e. growth and other seasonal variation, such as flowering) are viewed as probably some means of maintaining community diversity in the face of seasonal drought, infertile soils and periodic fire. Thus Kruger regards the observed growth patterns as having some adaptive advantage.

Growth is a complex process, and the same end result may well be achieved by

different means, under the one climate. A growth rhythm which developed under a different climate is likely to be maladapted to a changed climate. An inflexible growth rhythm is more likely to lead to extinction, once change occurs. Growth rhythms undoubtedly have a genetic component and are the product of a history, but the fact that they have survived climatic change, if one accepts that a summer growth rhythm originated in the tropics, should caution any who wish to attempt a backwards extrapolation.

The habitat

Lange (1982) includes the habitat as one of his lines of evidence for the reconstruction of the Tertiary vegetation. A considerable amount of information about the habitat is deduced from the fossil assemblage itself, hence the danger of a circular argument. Independent evidence about the habitat is found in the sediments themselves, the local depositional environment and the geological history of the region. Deductions about the habitat obtained from different fossil assemblages, e.g. animals, are a most valuable source of supporting speculation.

It appears, however, that Lange considers palaeogeography and oxygen-isotope palaeotemperatures as providing evidence of the habitat. These features are so general that their use in this way is rather like an ecologist defining habitat solely in terms of latitude and mean annual temperature. Such factors only constitute a background or regional setting. The more specific deductions about the habitat should be in general accord with the regional setting, but local factors may be of major importance in determining the overall specific character of the habitat.

DISCUSSION

Of all the lines of evidence, palaeobotany can do three things for the reconstruction of Tertiary vegetation which none of the others can do. These are:

1. Provide a time control, for fossils are datable,
2. Reveal extinct taxa and lineages, and
3. Show that taxa have occupied regions where they no longer grow.

Plant geography, phylogeny and other investigations from living plants can only suggest hypotheses which then require testing with independent evidence. If the hypothesis is an historical one, then the fossil record is the most important source of independent evidence. The reconstruction of vegetation from a fossil assemblage is a speculative process and it should be based on the evidence, viz, the fossils, the sediments, and the geological setting and history of the region where the fossils occur. To use investigations from living plants as evidence for the reconstruction of the Tertiary vegetation is to speculate upon mainly untested hypotheses, and this is not acceptable.

To plant geographers, phylogenists and others who wish to use the fossil record to deduce histories of the group(s) they study, the generalized nature of the fossil record will remain a problem. Even when a good record exists, rarely can it answer specific questions asked of it. For example, I am frequently asked when a specific taxon first appears in the fossil record. For the most part, I can only answer that the general pollen type is present, but it cannot be differentiated reliably from similar pollen, which may be found also in quite unrelated taxa, without the most detailed and intensive investigation.

Theoretically, the fossil record should pin-point the origin of a taxon in time and space, but there are practical difficulties to achieving this aim. If the taxon in question is found in isolated deposits, then the stratigraphic position and age may be difficult to establish. The 'resolution' in this case may be many millions of years, and it would appear that a taxon could become world wide in this time (for example, *Ilex*, a very

distinctive pollen type, see Martin, 1977). Some deposits are extensive and continuous through a relatively long period of time, and it is possible to trace evolutionary changes, as with the Atlantic Coastal Plain of the U.S.A. which has been used to trace the early evolution of angiosperm pollen (see Doyle, 1973, 1978). The experience with pollen referred to here would apply to macrofossils as well.

The future will witness many advances over the present knowledge of the Tertiary vegetation. New evidence will come to hand and older evidence will be viewed with new insight. Some outstanding problems such as the reasons for the presence of abundant *Nothofagus* with the *brassii* type pollen but the absence of leaves of this section of *Nothofagus* in the Tertiary fossil record of Australia, remain to be solved. The most fruitful investigations are likely to result from thorough studies of micro- and macrofossils in the same deposits and the sediments in which they occur, though, as discussed previously, few deposits are suitable for such investigations. There is much scope for innovative methods and the adoption of those used by Quaternary palaeoecologists (discussed previously), as Luly *et al.* (1980) have shown. Above all, interpretations must be based on basic physical and biological processes, and recognition of the numerous variables of the environment that influence plant distributions.

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